Spatial distribution and dispersal of spiders in a Danish barley field

Claus VANGSGAARD Dept. of Zoology, University of Aarhus, Universitetsparken, DK-8000 Aarhus C. Denmark.

Spatial distribution and dispersal of spiders in a Danish barley field. - Spiders were collected in pitfall traps in a transect running from a forest, through an unmanaged grass strip, into a field with spring sown barley. Plastic buckets were used to monitor ballooning activity. Numbers of species and specimens caught along the transect are described. Spatial distributions of the predominant species are illustrated. Dispersal patterns of these lycosid and linyphiid spiders are analysed and the importance of nearby habitats is discussed. It is concluded that the life cycles of the lycosids depended on the forest and the grass strip. However, the life cycles of the predominant linyphiids are not directly dependent on the nearby habitats.

INTRODUCTION

During the recent twenty years increasing interest has been paid to the importance of field edges and other nearby habitats for the dynamics of polyphagous predators in agricultural systems. The importance of polyphagous predators as control agents of pests in agricultural systems has been demonstrated by many authors (POTTS & VICKERMANN 1974, Edwards et al. 1979, Riechert & Lockley 1984). Impact of spiders on pest species in different crops have been analysed in a number of papers (See NYFFELER & BENZ 1987 for a review). And migration from field edges are studied in a number of papers on beetle migration (eg. DUELLI 1990, BLICK & BLISS 1991, LAGERLÖF & WALLIN 1993). However, only a few studies contributes to the knowledge of field edges as a potential reservoir for spiders (BISHOP 1981, VANGSGAARD et al. 1990, BAYRAM & LUFF 1993). Spider migration studies have mainly focused on ballooning activity (VAN WINGERDEN & VUGTS 1974, MEIJER 1977, DUFFEY 1956, 1978, GREENSTONE 1982, DEAN & STERLING 1985, AGNEW & SMITH 1989). However, the problems of interpreting ballooning data are considerable - eg. are the numbers net migration or is it just exchanges between different fields? Another problem concerns the fate of the individual spider. Did it only fly 10 metres or did it come from a distant habitat. Or was it just a mistake landing on the study area, so that it would have taken off if not collected by the scientist?

Manuscript accepted 10.01.1996.

Proceedings of the XIIIth International Congress of Arachnology, Geneva, 3-8-IX.1995.

CLAUS VANGSGAARD

As long as a practical methodology for interpreting ballooning data has not been worked out it seems that the only way of studying spider dispersal is to compare distribution patterns during spring and summer in transects running from field edges to field centres. This approach could reject the hypothesis of nearby habitats functioning as reservoirs or wintering areas of spiders. Topping & Sunderland 1995 described a method to interpret ballooning data, but further studies should confirm the applicability of their technical solution. The aim of this paper is to discuss effects of the field edges on the species composition in the field and to discuss movement patterns in different species. And further to discuss the very important question - do field edges help the spider community in controlling pest species?

STUDY AREA AND METHODS

The study was carried out on a field near Rønde, Jutland (56.17N,10.28E) belonging to the Danish Environmental Agency (DEA). The field "Stegelykke" was mainly used for studies on short and long term effects of pesticide spraying. The field was bordered to the west by the "Hestehave" forest (beech), a saltmarsh to the south, and east and north by other fields. Northern and southern field edges consisted of small gravel roads, whereas the eastern field edge was a main road edged with a hedge of old trees and shrubs. The spider fauna of the forest is known from a two year study by TOFT (1976). The study plot ran from 3 metres inside the Hestehave forest to the centre of the field. The vegetation of the field edge consisted of a mixture of different tree species outside the beech forest and a rich herbage layer. The unsprayed barley was sown on the 1. April and harvested on the 16. August. Spiders were collected in pitfall traps in a transect running from a forest, through a 2 metre broad unmanaged grass strip, into a field with spring sown barley. Seven rows of five pitfall traps were placed with rows at 3 metres into the forest, at the grass strip 1 metre from the field edge, and at a distance of 1, 5, 25, 50, and 75 metres into the field. The distance between traps in a row was 2 metre. The pitfall traps were made of plastic and had a diameter of 65 mm and were 10 cm deep. Each trap were half-filled with a saturated water solution of benzoic acid and a detergent. Ballooning activity was monitored by means of 3 plastic buckets and the same trapping fluid. These buckets were placed on the ground 25, 50, and 75 metres inside the field. The vegetation around the buckets where removed to prevent spiders dropping from the crop into the buckets. The traps were sampled every week from the 5. March to harvest on the 12. of August.

Spiders were identified using LOCKET & MILLIDGE (1953), ROBERTS (1985, 1987), and HEIMER & NENTWIG (1991). All adult spiders were identified to species and juveniles to family or genus level. The nomenclature used was that of MERRETT *et al.* (1983). However, a small numbers of species not included in the British fauna were named following HEIMER & NENTWIG (1991).

Differences between rows were studied by means of an index of similarity: S=2c/a+b, where c is the number of species common to both rows and a and b are the

total number of species in each row. Relative "mean position" from field edge of important species was computed from the expression

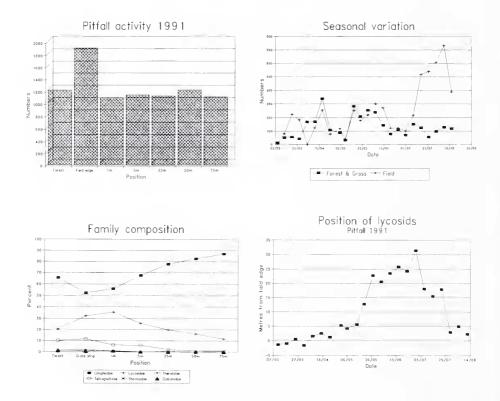
$$P = \frac{\sum_{N_{tot}} (P_i N_i)}{N_{tot}}$$

where Ni is the number of individuals in trap row i, Pi is the distance from the field edge, and Ntot is the total number of individuals of that species (VANGSGAARD *et al.* 1990). These "mean positions" were computed for each trapping period and as an average for the trapping season. Principal Component Analysis were used for indirect ordination. The software used was CANOCO (BRAAK 1988) for ordination and CANODRAW for graphical output (SMILAUER 1990).

RESULTS

A total of 8709 specimens of 124 species were collected in 1991. The 124 spider species represented 15 families. Juveniles, that were identified to family or if possible to genus, accounted for about 15% of the total numbers. Ballooning activity was low in 1991, where only 120 specimens of 20 species were caught. B.gracilis, which is the dominant spider in the highest part of the barley crop, accounted for 40% of the spiders caught. The pitfall trap catches of spiders was evenly distributed over the transect except activity was higher in the grass strip (fig.1). However, the activity in the field increased during the growing season whereas activity declined in the forest and at the grass strip (fig.2). Numbers of species declined from the field edge to the centre of the field. Further, there was a shift in dominance between different families from the forest to the field centre (fig.3). The relative numbers of linyphilds were 65% in the forest, 52% at the grass strip, and it rose to 87% in the centre of the field. This increase in linyphiid numbers was followed by a corresponding decrease in wolf spiders. The Tetragnathidae (only Pachyguatha species) were important in the forest and at the grass strip, but the relative numbers declined from about 10% to 5% at the 1 and 5 metre rows and further down to about 2% in the centre of the field. The relative abundance of linyphiids increased during summer from 51% in mid-april to more than 80% in August due to the dominant species such as *E.atra* and *Oe.apicatus*. The relative abundance of lycosids rose from about 10% in April to more than 40% in mid June.

The dominant species were *Pachygnatha listeri* Sundevall,1830, *Diplocephalus piciuus* (Blackwall,1841), *D.latifrons* (O.P.-Cambridge,1863) in the forest. *Pardosa lugubris* (Walckenaer,1802), *Pachygnatha listeri*, *Pelecopsis radicicola* (L. Koch,1872), *D.latifrons* and *D.piciuus* dominated in the grass strip. *Bathyphautes gracilis* (Blackwall,1841) and *Pardosa lugubris* dominated in the field margin (1 metre and 5metre rows), and *Erigone atra* Blackwall,1883, *Meioneta rurestris* (C.L. Koch,1836), and *Oedothorax apicatus* (Blackwall,1850) in the centre of the field. However, two species - *E.atra* and *Oe.apicatus* - accounted for more than one-third of the total numbers caught.



FIGS 1-4

Fig. 1: Pitfall activity 1991; Number of individuals caught in the different pitfalls from March to August; Fig. 2: Seasonal variation in spider numbers caught inside versus outside the field;Fig. 3: Family composition; relative numbers of the most important spider families caught in the different pitfall rows; Fig. 4: Position of lycosids; wolf spider dispersal into the field. The represented points are the mean position of all wolf spiders.

The position of lycosids (fig.4) shows a shift from the forest edge to the centre of the field from May to June. This was especially evident in *Pardosa prativaga* (L. Koch, 1870), and, to a lesser extent, *Trochosa ruricola* (Degeer, 1778) and *P.lugubris*. The dominant linyphiids showed no seasonal dispersal patterns. Table 2 shows the average position of the populations of some important linyphiids and lycosids. A position value higher than 22.3 means that the population are less numerous near the field edge, and contrary, a value smaller than 22.3 means that the species are more numerous near the edge. The two *Oedothorax* species have the highest values, but also the *Erigone* species and *Meioneta rurestris* have values above 30. *Bathyphantes gracilis* have an evenly distribution over the field. *Lepthyphantes tenuis* (Blackwall, 1852) tends to be more numerous near the field edge (a value of 10.6).

		O	1

		5					
	Forest	Grass	1 metre	5metre	25metre	50metre	75metre
Forest		0,77	0,71	0.54	0,39	0,41	0,37
Grass	0,77	-	0,61	0,59	0,43	0,41	0,36
1 metre	0,71	0,61	-	0,75	0,59	0,58	0,51
5metre	0,54	0,59	0,75	-	0.67	0,64	0,51
25metre	0,39	0,43	0.59	0,67	-	0,76	0,59
50metre	0,41	0,41	0,58	0,64	0,76	-	0,67
75metre	0,37	0,36	0,51	0,51	0,59	0,67	-

I ABLE I	Τ	ABLE	1
----------	---	------	---

Similarity between the rows of the transect

As supposed similarity between rows declined with increased distance (Table 1). There was a high similarity between the forest and the grass strip and between the field rows. However, there was a tendency towards an edge zone with similarities between the 1metre and 5metre rows higher than between the 5metre and 25metre rows. Principal Component Analysis revealed a clear grouping of spiders (fig.5). The typical agricultural spiders such as Pardosc prativaga, Erigone atra, Oedothorax *apicatus* and *Meioneta rurestris* are placed close together in the 2. square. The spiders from the grass stripe were represented in the first square and the spiders from within the forest in the fourth square. The PCA-plot of sites (fig.5) follows closely the results from the species plot. The forest site is in the 4. square, the edge site in the 1. square and the remaining sites are placed in a row from the 2. to the 3. square. The order of the sites follows the increasing distance to the edge.

TABLE 2

Mean position of the population of important linyphild and lycosid species and their numbers in the adjacent areas.

Species	Forest	Edge	Position	Total numbers
Oedothorax apicatus	1	4	46.01	1339
Oedothorax fucsus	0	0	46.00	67
Bathyphantes gracilis	2	15	22.90	250
Lepthyphantes tenuis	9	22	10.60	77
Erigone atra	14	44	30.45	1594
Erigone dentipalpis	2	1	31.89	254
Meioneta rurestris	$\overline{2}$	2	35.39	233
Pardosa lugubris	44	107	4.60	280
Pardosa prativaga	6	17	30.69	361
Trochosa ruricola	37	79	11.26	291

DISCUSSION

The importance of nearby habitats for polyphagous predators has been stressed by several studies. Especially the forest ecotone has been the subject of a number of studies that states that they hold a larger numbers of species than the centre of the forest (eg. LUCZAK 1991, BLICK & BLISS 1991, HÄNGGI 1991). Further, some studies have tried to increase numbers of beneficial arthropods by establishing within field stripes (THOMAS et al. 1992). These should ease dispersal into the field. However, the question is if the arthropods living in these stripes will penetrate into the field and subsequently establish a population. Studies on carabids shows a positive response to increasing numbers of nearby habitats (THOMAS et al., 1992, COOMBES & SOTHERTON 1986). Several studies on habitat requirements and migration of wolf spiders shows a pattern with a wintering area and a spring migration into adjacent fields. The overwintering habitats of wolf spiders were studied by NØRGAARD (1951), Edgar (1970), EDGAR & LOENEN (1974), and BAYRAM & LUFF (1993). They concluded that grass, and especially grass tussocks, are important shelters in the winter period. The dispersal patterns of lycosids were studied by RICHTER (1970) and VANGSGAARD et al. (1990), and DENNIS (1991) concluded that as the aeronautic activity of lycosids are low, their ability to migrate into the field are less than the more aeronautic linyphiids. However, VANGSGAARD et al. (1990) showed that the dispersal speed of a population of Pardosa lugubris was 2 meters per day. So small to medium sized fields would be covered within a month.

This study confirms the overall dispersal patterns of the lycosids (fig.5). However, there was some contradictions between this and the other Danish study on the dispersal of Pardosa lugubris (VANGSGAARD et al. 1990). In the present study it remained close to the field edge and did not penetrate the field centre. The explanation might be that the former study was carried out on a relative small field completely surrounded by forest or that the mixed crop in the studied field created an environment more suitable for P.lugubris. In Switzerland HÄNGGI (1991) showed that P.lugubris did not penetrate more than a few metre into a meadow from the surrounding forest. In the present study other wolf spider species eg. P. prativaga and Trochosa ruricola moved into the field, and especially juveniles moved fast into the field. Other Pardosa species (P.palustris, P.agrestis, P.amentata (Clerck, 1757), P.monticola (Clerck, 1757), P.nigriceps (Thorell, 1856), and P.pullata (Clerck, 1757)) were only found in the field, but this must be explained by their dispersal into the field as juveniles. Identification of juveniles would then be necessary to verify dispersal patterns of these species. However, the overall dispersal patterns of juveniles support the idea of a general dispersal of lycosids into the field.

From mid July a dispersal pattern of lycosids out of the field was seen. This could be explained by the females searching for suitable areas for rearing her offspring. The effect of wolf spider predation on pest species would then be strongest in June and July. However, as NYFFELER & BENZ (1988) stated, the numbers of wolf spiders and their relative low capture rate predicted that the effect on the pest species were of minor importance. Population numbers of wolf spiders are very difficult to

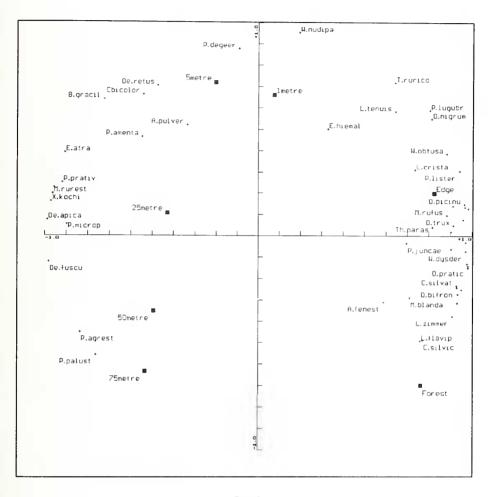


Fig. 5

Principal component analysis of species and sites.

estimate in the field, but probably the maximum densities are between 1 and 10/m2 (NYFFELER & BENZ 1988, SAMU & SAROSPATAKI 1995). These numbers are much lower than the densities of linyphiids with more than 500/m2 at maximum (TOFT *et al.* 1995). Although this wolf spider predation might be well synchronized with the life cycles of aphid species in Danish crops it seems uncapable of controlling the aphid numbers.

It seems evident that lycosids disperse into the field from habitats outside the field, but the question of linyphild dependence on habitats outside the field is less obvious. Toft et al. (1995) showed that rotation and sowing in spring reduced spider density to less than 10%; so the spider fauna are a mixture of survivors, their off-

CLAUS VANGSGAARD

spring and spiders dispersing into the field. Although only 3 buckets were used to monitor spider ballooning it gave an indication of that ballooning activity had a minor importance in the distribution of spiders during spring and summer. If we pool all the 1991 data, ballooning activity would give a total precipitation of 3.78 spiders m⁻². If the important linyphilds depended on the field edge we would expect to find a dispersal pattern from the grass strip into the field. This was not the case as it seems that throughout the period the numbers of these spiders declined as we move closer to the edge. It is consistent with the finding that only a few of these spiders were caught in the forest and at the grass strip. It seems that some of the species are avoiding the area close to the field edge - at least the inner 5 metres. Especially Oedothorax apicatus showed this pattern as only 5 specimens (0.4%) of this species were caught in the forest and at the grass strip. This is supported by the findings of NYFFELER & BREENE (1992) who concluded that densities of *E.atra*, *E.dentipalpis* and *Oe.apicatus* were higher in the centre of a Swiss winter wheat field. This could lead us to the conclusion that increasing the numbers of linyphilds is not obtained by providing more within field habitats of this type. In a further Swiss study HÄNGGI (1991) showed that forest dwelling spider species did not penetrate more than 10 metre into a meadow. In Poland LUCZAK (1991) stated that the forest ecotone acted as a barrier to dispersal into the surrounding fields. However, it seems to be a statement without taking in account the knowledge about the typical spider fauna of field systems. The typical spider species in fields are usually not originating from forest systems but from more open habitats. If the forest ecotone were artificially removed the numbers of spiders from the forest might increase in the adjacent metres of the field. But it would be very risky to predict that these spider species would disperse and establish substantial populations in the centre of the field.

The very common use of pitfall traps have been discussed in several papers (UETZ & UNZICKER 1976, TOPPING & SUNDERLAND 1992, TOPPING 1993, DINTER 1995, TOFT *et al.* 1995, ULBER & WOLF-SCHWERIN 1995, SUNDERLAND *et al.* 1995). They state that results from pitfall catches should be interpreted with cautiousness as numbers caught are a result of several factors. Important factors are density, activity, season, habitat structure, and species differences in respond to the pitfall traps. However, the pitfall traps are usefull in comparing distributional patterns and for studies on phenology and faunistics. In the present study there might be problems in interpreting pitfall catches in the field versus outside the field as the activity of the spiders might be affected by the structural differences between the two habitats.

The ideas of establishing within field habitats for increasing the density of spiders and other polyphagous predators seems to be partly supported by this study. However, this is only evident in lycosids as it was impossible to establish a connection between the linyphild spider fauna of the field and the surrounding habitats. In Sweden LAGERLÖF & WALLIN (1993) showed that the floristic composition of field margins affected the spider activity significantly. It might be that other types of field margins could increase numbers of linyphilds but the finding that the most important species seems to avoid the forest and grass strip do not look promising. And so far it has not been possible to find any publication of evidence of linyphilds dispersing

from unmanaged habitats to field systems. Although there is no direct dependence of the field edges there might be an indirect effect, eg. the field edges providing prey species in certain critical periods of the season. But still the mechanisms behind the population dynamics between natural and cultivated areas are not sufficiently understood. What we need are detailed studies on population dynamics at species level before we can quantify and model the interactions between the field and the surrounding areas.

SPECIES LIST 1991 AMAUROBIIDAE Amaurobius fenestralis (Stroem, 1768) DICTYNIDAE Lathys humilis (Blackwall, 1855) **GNAPHOSIDAE** Zelotes subterraneus (C.L.Koch, 1833) Z. lutetianus (L.Koch, 1866) Z. pusillus (C.L.Koch, 1833) MICARIDAE *Micaria pulicaria* (Sundevall, 1832) Micaria aenea Thorell CLUBIONIDAE Chubiona reclusa O.P.-Cambridge, 1863 C. pallidula (Clerck, 1757) C. terrestris Westring, 1851 C. compta C.L.Koch, 1839 C. diversa O.P.-Cambridge, 1862 ZORIDAE Zora spinimana (Sundewall, 1833) THOMISIDAE Xysticus cristatus (Clerck, 1757) X. kochi Thorell,1872 X. lanio C.L.Koch, 1835 X. *ulmi* (Hahn, 1831) Ozyptila praticola (C.L.Koch, 1837) O. trux (Blackwall, 1846) **PHILODROMIDAE** Thanatus striatus C.L.Koch,1845 LYCOSIDAE Pardosa agrestis (Westring, 1861) P. purbeckensis F.O.P.-Cambridge, 1895 P. monticola (Clerck, 1757) P. palustris (Linnaeus, 1758) P. pullata (Clerck, 1757) P. prativaga (L.koch, 1870) P. amentata (Clerck, 1757) P. nigriceps (Thorell, 1856) P. lugnbris (Walckenaer, 1802) P. paludicola (Clerck, 1757) Alopecosa pulvernlenta (Clerck, 1757) Trochosa ruricola (Degeer, 1778) T. terricola Thorell, 1856 PISAURIDAE Pisaura mirabilis (Clerck, 1757)

AGELENIDAE Circurina circur (Fabricius, 1793) Cryphaeca silvicola (C.L.Koch, 1834) HAHNIIDAE Hahnia montana (Blackwall, 1841) Mimetidae Ero furcata (Villers, 1789) THENIDIIDAE Crustulina guttata (Wider, 1834) Theridion sisyphium (Clerck, 1757) T. bimaculatum (Linnaeus, 1767) Robertus lividus (Blackwall, 1836) R. neglectus (O.P.-Cambridge,1871) Enoplognatha ovata (Clerck, 1757) E. thoracica (Hahn, 1833) Tetragnathidae Pachygnatha clercki Sundevall, 1823 P. listeri Sundevall, 1830 P. degeeri Sundevall, 1830 LINYPHIDAE Ceratinella brevipes (Westring, 1851) C. brevis (Wider, 1834) Walckenaeria acuminata Blackwall, 1833 W. alticeps (Denis, 1952) W. cucullata (C.L.koch, 1836) W. dysderoides (Wider, 1834) W. nudipalpis (Westring, 1851) W. obtusa Blackwall, 1836 W. atrotibialis (O.P. Cambridge, 1878) W. unicornis (O.P.-Cambridge, 1861) Entelecara acuminata (Wider, 1834) Dicymbium nigrum f. brevisetosum Locket,1962 D. tibiale (Blackwall, 1836) Gongylidium rufipes (Sundewall, 1829) Dismodicns bifrons (Blackwall, 1841) Gonatium rubens (Blackwall, 1833) G. rubellum (Blackwall, 1841) Maso sundewalli (Westring, 1851) Pocadicnemis juncae Locket & Millidge, 1953 Oedothorax fuscus (Blackwall, 1834) O. retusns (Westring, 1851) O. apicatus (Blackwall, 1850) Pelecopsis radicicola (L.Koch, 1872) Cnephalocotes obscurus (Blackwall, 1834)

CLAUS VANGSGAARD

Troxochrus scabricolus (Westring, 1851) Minyriolus pusillus (Wider, 1834) Tapinocyba pallens (O.P.-Cambridge, 1872) Thyreostenius parasiticus (Westring, 1851) Monocephalus carstaneipes (Blackwall, 1834) Mioxena blanda (Simon, 1884) Saloca diceros (O.P.-Cambridge, 1871) Gongylidiellum vivum (O.P.-Cambridge, 1875) Micrargus herbigradus (Blackwall, 1844) *M. apertus* (O.P.-Cambridge, 1871) Erigonella hiemalis (Blackwall, 1841) Savignia frontata (Blackwall, 1833) Diplocephalus latifrons (O.P.Cambridge, 1863) D. picinus (Blackwall, 1841) Araeoncus humilis (Blackwall, 1841) *Erigone dentipalpis* (Wider, 1834) E. atra Blackwall, 1833 E. longipalpis (Sundevall, 1830) Porrhomma microphthalmum (O.P.-Cambridge, 1871) Porrhomma lativela Tretzel P. egeria Simon, 1884 P. montanum Jackson, 1913 Agyneta sp. *Meioneta rurestris* (C.L.Koch, 1836) M. viaria (Blackwall, 1841)

Centromerus sylvaticus (Blackwall, 1841) *Centromerus dilutus* (O.P.-Cambridge, 1871) C. incilium (L.Koch, 1881) Centromerus sp. Tallusia experta (O.P.-Cambridge, 1871) *Centromerita bicolor* (Blackwall, 1833) Saaristo abnormis (Blackwall, 1841) Macragus rufus (Wider, 1834) *Bathyphantes gracilis* (Blackwall, 1841) B. nigrinus (Westring, 1851) Diplostyla concolor (Wider, 1834) Lepthyphantes alacris (Blackwall, 1853) L. tenuis (Blackwall, 1852) L. zimmermanni Bertkau, 1890 L. cristatus (Menge, 1866) L. mengei Kulczynski, 1887 L. flavipes (Blackwall, 1854) *L. tenebricola* (Blackwall, 1854) L. ericaeus (Blackwall, 1853) L. pallidus (O.P.-Cambridge, 1871) L. insignis (O.P.-Cambridge, 1913) L. angulatus (O.P.-Cambridge, 1881) *Neriene clatlırata* (Sundewall,1830) Linyphia hortensis Sundewall,1830 *Microlinyphia pusilla* (Sundewall, 1829)

REFERENCES

- AGNEW, C.W. & SMITH, J.W. 1989. Ecology of Spiders (Araneae) in a Peanut Agrosystem. Environmental Entomology 18(1):30-42.
- BAYRAM, A. & LUFF, M.L. 1993. Winter abundance and diversity of lycosids (Lycosidae, Aranea) and other spiders in grass tussocks in a field margin. *Pedobiologia* 37:357-364.
- BISHOP, A.L. 1981. The spatial distribution of spiders in a cotton ecosystem. *Australian Journal* of Zoology 29:15-24.
- BLICK, T. & BLISS, P. 1991. Spinnentiere und Laufkäfer am Waldrand (Arachnida: Araneae, Opiliones, Pseudoscorpiones; Insecta:Coleoptera:Carabidae). Bulletin de la Société neuchateloise des Sciences naturelles 116(1):25-34.
- BRAAK, C.J.F.ter, 1988. CANOCO a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical correspondence analysis and redundancy analysis (Version 2.1)]. *Technical report LWA 88-02, Groep Landbouwiskunde, Wageningen.*
- COOMBS, D.S. & SOTHERTON, N.W. 1986. The dispersal and distribution of polyphagous predatory Coleoptera in cereals. *Annals of Applied Biology* 108:461-471.
- DEAN, D.A. & STERLING, W.L. 1985. Size and phenology of ballooning spiders at two locations eastern Texas. *Journal of Arachnology* 13:111-120.
- DENNIS, P. 1991. The temporal and spatial distribution of arthropod predators of the aphids *Rhopalosipluum padi* (W.) and *Sitobion avaeane* (F.) in cereals next to field-margin habitats. *Norwegian Journal of Agricultural Science* 5:79-88.
- DINTER, A. 1995. Estimation of epigeic spider population densities using an intensive D-vac sampling technique and comparison with pitfall trap catches in winter wheat. *Acta jutlandica* 70(2):23-32.

- DUELLI, P. 1990. Population Movements of Arthropods between Natural and Cultivated Areas. *Biological Conservation* 54:193-207.
- DUFFEY, E. 1956. Aerial dispersal in a known spider population. *Journal of Animal Ecology* 25:85-111.
- DUFFEY, E. 1978. Ecological strategies in spiders including some characteristics of species in pioneer and nature habitats. *Symposia of the Zoological Society of London* 42:109-123.
- EDGAR, W.D. 1970. Prey and feeding behaviour of adult females of the wolf spider Pardosa amentata (Clerck). *Netherlands Journal of Zoology* 20:487-491.
- EDGAR, W. & LOENEN, M. 1974. Aspects of the overwintering habitat of the Wolf spider *Pardosa lugubris. Journal of Zoology* 172:383-388.
- EDWARDS, C.A., SUNDERLAND, K.D. & GEORGE, K.S. 1979. Studies on polyphagous predators of cereal aphids. *Journal of applied Ecology* 16:811-823.
- GREENSTONE, M. 1982. Ballooning frequency and habitat predictability in two wolf spider species (Lycosidae:Pardosa). *Florida entomologist* 65(1):83-89.
- HÄNGGI, A. 1991. Minimale Flächengrösse zur Erhaltung standorttypischer Spinnengemeinschaften -Ergebnisse eines Vorversuches. Bulletin de la Societe neuchâteloise des Sciences naturelles 116(1):105-112.
- HEIMER, S. & NENTWIG, W. 1991. Spinnen Mitteleuropas Ein Bestimmungsbuch. Paul Parey. Berlin, Hamburg.
- LAGERLÖF, J. & WALLIN, H. 1993. The abundance of artropods along two field margins with different types of vegetation composition: an experimental study. Agriculture, *Ecosystems and Environment* 43:141-154.
- LOCKETT, G.H. & MILLIDGE, A.F. 1953. British Spiders I & II. Ray Society, London.
- LUCZAK, J. 1991. Ecotone zones between forest island and crop fields in the Masurian Lakeland, Poland, as barriers for migration of spiders to cropfields. Bulletin de la Société neuchâteloise des Sciences naturelles 116(1):161-167.
- MEUER, J. 1977. The immigration of spiders (Araneida) into a new polder. *Ecological Ento*mology 2:81-90.
- MERRET, P., LOCKETT, G.H. & MILLIDGE, A.F. 1983. A check list of British Spiders. *Bulletin of the British Arachnological Society* 6(9):381-403.
- NØRGAARD, E. 1951. On the ecology of two lycosid spiders (Pirata piraticus and Lycosa pullata) from a Danish Sphagnum bog. *Oikos* 3:1-21.
- NYFFELER, M. & BENZ, G. 1987. Spiders in natural pest control: A review. *Journal of applied Entomology* 103:321-339.
- NYFFELER, M. & BENZ, G. 1988. Feeding ecology and predatory importance of wolf spiders (*Pardosa* spp.)(Aranea,Lycosidae) in winter wheat fields. *Journal of applied Entomology* 106:123-134.
- NYFFELER, M. & BREENE, R.G. 1992. Dominant insectivorous polyphagous predators in winter wheat: high colonization power, spatial dispersion patterns, and probable importance of the soil surface spiders. *Deutsche entomologische Zeitschrift*, N.F. 39:1-3,177-188.
- POTTS, G.R. & VICKERMANN, G.P. 1974. Studies on the cereal ecosystem. Advances in Ecological Research 8:107-197.
- RICHTER, C.J.J. 1970. Aerial dispersal in relation to habitat in eight wolf spider species (*Par-dosa*, Araneae, Lycosidae). *Oecologia* 5:200-214.
- RIECHERT, S.E. & LOCKLEY, T. 1984. Spiders as biological control agents. Annual Review of Entomology. 29:299-320.
- ROBERTS, M.J. 1985. The spiders of Great Britain and Ireland. Volume 1. Harley Books, Colchester, England.
- ROBERTS, M.J. 1987. The spiders of Great Britain and Ireland. Volume 2. Harley Books, Colchester, England.

- SAMU, F. & SAROSPATAKI, M. 1995. Estimation of population sizes and "home ranges" of polyphagous predators in alfalfa using mark-recapture: an exploratory study. Acta jutlandica 19:47-55.
- SMILAUER, P. 1990. CANODRAW. A companion program to CANOCO for publication-quality graphical output. *Ithaca*.
- SUNDERLAND, K.D., DE SNOO, G.R., DINTER, A., HANCE, T., HELENIUS, J., JEPSON, P., KROMP, B., LYS, J.-A., SAMU, F., SOTHERTON, N.W., TOFT, S. & ULBER, B. 1995. Density estimation for invertebrate predators in agroecosystems. *Natura jutlandica* 19:5-40.
- THOMAS, M.B., WRATTEN, S.D., & SOTHERTON, N.W. 1992. Creation of "island" habitats in farmland to manipulate populations of beneficial arthropods: predator densities and species composition. *Journal of Applied Ecology* 29(2):524-531.
- TOFT, S. 1976. Life-histories of spiders in a Danish beech wood. Acta jutlandica 19:5-40.
- TOFT, S., GOLDSMIDT, H., & VANGSGAARD, C. 1995. Distance methods used to estimate densities of web spiders in cereal fields. *Acta jutlandica* 70(2):133-162.
- TOPPING, C.J. 1993. Behavioural responses of three linyphild spiders to pitfall traps. *Ento*mologia Explicata Applicata 68:287-293.
- TOPPING, C.J. & SUNDERLAND, K.D. 1992. Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. *Journal of applied Ecology* 29: 485-491.
- TOPPING, C.J. & SUNDERLAND, K.D. 1995. Methods for monitoring aerial dispersal by spiders. Acta jutlandica 70(2):245-256.
- UETZ, G.W. & UNZICKER, J.D. 1976. Pitfall trapping in ecological studies of wandering spiders. Journal of Aracluology 3:101-111.
- ULBER, B. & WOLF-SCHWERIN, G. 1995. A comparison of pitfall catches and absolute density of carabid beetles in oilseed rape fields. *Acta jutlandica* 70(2):77-86.
- VAN WINGERDEN, W.K.R. & VUGTS, H.F. 1974. Factors influencing aeronautic behaviour of spiders. *Bulletin of the British Arachnological Society* 3:6-10.
- VANGSGAARD, C., GRAVERSEN, E., & TOFT, S. 1990. The spider fauna of a marginal agricultural field. *Entomologiske Meddelelser* 58(2):47-54.